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RECONSTITUTION OF COELOMETOPINI, TENEBRIONINI AND RELATED TRIBES OF AMERICA NORTH OF COLOMBIA (COLEOPTERA: TENEBRIONIDAE)

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Abstract.—The tenebrionid subfamilies Tenebrioninae and Coelometopinae are diagnosed. The tenebrionine tribes Tenebrionini and Alphitobiini are defined, and most genera previously included in Tenebrionini are transferred to Coelometopini. Centronopini and Acropteronini are proposed as new tribes of Tenebrioninae. The coelometopine tribes Coelometopini, Strongyliini and Talanini are defined. Cnodalonini, Misolampini and Nodotelini have been based on superficial characters which primarily reflect loss of flying ability. Each of these groups consists of paraphyletic assemblages derived several times independently from Coelometopini, and they are placed as junior synonyms of that tribe. Keys are provided to the genera of these beetles for North and Central America.

Since the work of Lacordaire (1859) members of two major lineages (tenebrionine and coelometopine lineages of Doyen and Tschinkel, 1982) of Tenebrionidae have been confounded and included in the tribe Tenebrionini. Lacordaire recognized the difficulty in defining his Tenebrionini and specifically addressed its apparent relationship to Cyphaleini (= Heleini) and Cnodalonini (also to Pycnocerini). Heleini is very similar to Tenebrionini (Doyen et al., in press; Matthews and Doyen, in press), constituting part of the Tenebrionine lineage of Doyen and Tschinkel (1982), whereas Cnodalonini forms part of the Coelometopine lineage. These two lineages consistently differ in the configuration of the internal female reproductive tract, ovipositor, defensive glands and reservoirs, and other features (Tschinkel and Doyen, 1980). Other character differences are less constant (e.g., tarsal vestiture; aedeagal orientation; maxillary structure). The primary features used by Lacordaire for separating these groups (armature of maxillary lacinia; shape of mesosternum, etc.) belong to the second group of characters, and do not vary in concordance with tribal limits based on the female reproductive tract and other characters mentioned above. Lacordaire (1859:366) remarked upon the variability of these tribes, both in morphological and biological characteristics. Surprisingly he commented only briefly (p. 359) on their relationship to his Coelometopides, whose chief unifying feature is loss or great reduction of the wings.

Subsequent to Lacordaire's work, no formal definitions have been provided for any of these tribes. Genera have been assigned on the basis of external characters alone, resulting in some preposterous classifications. For example, as pointed out by Spilman (1962b) *Zophobas,* which is winged, is always included in Tenebrionini, while *Rhinandrus,* which is wingless, is placed in Coelometopini. All important characters indicate that they are sister genera within Tenebrionini. Similarly, *Coelocnemis* differs from *Iphthiminus* primarily by loss of wings (Doyen, 1973), but this very feature places the two in different tribes.

Based on characters of the internal female reproductive tract, ovipositor, defensive reservoirs and various external features, most genera now included in Tenebrionini are here transferred to Coelometopini, which is expanded to include Misolampini and Cnodalonini. In this sense Coelometopini is one of the larger and more diverse tribes of Tenebrionidae, consisting mostly of tropical and subtropical forms which are associated with decaying wood. Larvae of Strongyliini, the other major tribe of Coelometopinae, also inhabit rotten wood. The coelometopine lineage is formally defined below as the subfamily Coelometopinae.

In contrast, Tenebrionini is reduced to a small, relatively uniform group, whose larvae, with the exception of *Bius,* are scavengers on animal or non-ligneous plant remains. *Alphitobius* (formerly in Triboliini) and *Metaclisa marginalis* (formerly in Cnodalonini are here placed in Alphitobiini, which differs from Tenebrionini in several external features, notably antennal sensory structures. The position of these taxa has long been uncertain, as indicated by Reitter's original (1917) proposal of Alphitobiini and his (1922) placement of *Metaclisa* in Scaphidemini.

Acropteronini is proposed for *Acropteron,* presently in Cnodalonini. *Acropteron* shows most of the diagnostic features of Tenebrioninae, but does not conform to any of the existing tribes. Its most notable characters are the presence of 10 elytral striae, internally open procoxal cavities (both primitive) and a highly derived ovipositor.

Centronopus and *Scotobaenus* are superficially similar to certain Coelometopini (Lacordaire believed they resembled *Menephilus*), but lack the distinctive coelometopine female reproductive tract and ovipositor. They differ from other tribes of Tenebrioninae in defensive reservoir structure and other characters. Hence the tribe Centronopini is proposed. All of these tribes are placed in the subfamily Tenebrioninae, which is formally defined.

Detailed discussions of character interpretation and apparent relationships among the taxa addressed briefly above are given where appropriate below. Morphological terminology follows usage in Tschinkel and Doyen (1980) and Doyen and Tschinkel (1982). The geographic scope is America north of Colombia with occasional reference made to other areas. Table 1 provides a conspectus of the included taxa and taxonomic changes.

Several genera which appear in catalogues are excluded from Table 1 because they have previously been moved into other tribes of Tenebrionidae or into other families. These are: 1) *Adelonia* Laporte, transferred into Belopini (Doyen and Tschinkel, 1982; Doyen, 1988); *Merotemnus* Horn and *Rhacius* Champion are junior synonyms of *Adelonia* (Spilman, 1961). 2) *Alaephus* Horn, transferred into Vacronini (Doyen and Lawrence, 1979). 3) *Boros* Herbst, separated as Boridae (Crowson, 1955). *Eupsophulus* Cockerell (=*Eupsophus* Horn), transferred to Vacronini (Doyen and Lawrence, 1979). 4) *Biomorphus* Motschulsky has been placed in synonymy under *Helops* Fabricius (Aalbu et al., in press).

In addition *Maracia haagi* Gebien is listed from Central America by Papp (1961). Gebien (1919:35) states, however, that the type locality is unknown, and *Maracia* has not been subsequently mentioned in the primary literature. It is not considered here. *Reminius* Casey was placed in synonymy under *Strongylium* by Spilman (1959). *Pteroglymmius* Gebien is a synonym of *Isaminas* Champion (Doyen, 1987). *Paroeatus* is listed by Papp (1961) as possibly from Central America. It is included in Table 1 and the keys even though I have seen specimens only from South America.

Hesiobates, described from Dominican amber by Kaszab (1984) appears to belong in Coelometopini, and may be closely related to *Hesiodus, Ilus* and *Choastes.* It is not considered further in this work.

Tenebrioninae

Description. Adult.—Small to large (about 3 mm to 30 mm). Antennae filiform-serrate, incrassate or rarely capitate bearing only simple, setiform sensilla or occasionally with compound, stellate sensoria on apical five or six segments. Labrum transverse with basal membrane exposed or concealed. Mandible with mola striate or not. Maxilla with galea finely setose or with uncus of one or two teeth. Tentorium with bridge posterior, flat or arched. Procoxal cavities closed externally, open or closed internally. Mesocoxal cavities closed laterally by mesepimeron or sternum. Elytra with scutellary striole and 9 complete striae or estriate. Apical membrane comprising 25% of less of wing length; recurrent cell large to small or obsolete; subcubital fleck present or absent. Metendosternite usually with long stalk, long arms with subterminal muscle attachment flange; tendons inserted near midpoint or toward apex. Tarsi usually with ventral surface coarsely setose or spinose, occasionally with pads of pilose setae. Ovipositor usually with coxites clearly 4-lobed, occasionally with ovipositor shaft shortened and lobing reduced; lobes usually subequal in length; fourth lobe rarely free and digitate; paraprocts parallel to axis of ovipositor at rest. Internal female reproductive tract consisting of vagina, bursa copulatrix, long slender spermathecal accessory gland and spermatheca. Aedeagus with tegmen dorsal or rotated about 45° to 90° at rest, rarely inverted; median lobe freely extrusible or adnate to tegmen; sometimes with accessory lobes. Defensive reservoirs variable, often distinctive at tribal level (see Tschinkel and Doyen, 1980).

Larva.—Variable in all important characters (see discussion below).

Tenebrioninae corresponds to the combined tenebrionine, toxicine and opatrine lineages recognized by Doyen and Tschinkel (1982). This group includes those tribes in which the spermatheca is derived from the bursa copulatrix, and appears as a separate structure from the spermathecal accessory gland. (Alleculinae, which usually have this configuration, are recognized here as a separate subfamily.)

Discussion. The ovipositors of this group are mostly similar to that of *Tenebrio,* with the paraproct subequal to the coxite and the coxite composed of four similar lobes. However, in Toxicini and Boletophagini, the fourth ovipositor lobe is free and digitate, as in Lagriini; in some Toxicini there are several bursa-derived spermathecae, again resembling Lagriinae. Among Alleculinae, which mostly conform to the tenebrionine pattern, *Lobopoda* has both ovipositor and internal female reproductive structures similar to Lagriinae. These character distributions suggest that the tenebrionine configurations may have been evolved independently more than a single time. There are also enormous differences in life style and habits of various tenebrionine tribes, however, which could indicate that some of these structural patterns (especially in ovipositor morphology) have arisen as secondary specializations from the basic tenebrionine configuration described above. For example, the ovipositors of Boletophagini and Toxicini, which both inhabit fruiting bodies of polypore fungi, are similar in structure to the ovipositors of many Diaperini (but not *Diaperis*), which also live on fungi. In contrast, the ovipositors of Eleodini and Opatrini (also Tenebri-

Table 1. Tribal placements of North and Central American genera treated in text. Former placement indicated at right.

Alphitobiini	
Alphitobius Stephens	Triboliini
Metaclisa J. DuVal	Cnodalonini
Tenebrionini	
Bius Motschulsky	Tenebrionini
Idiobates Casey	Tenebrionini
Neatus LeConte	Tenebrionini
Rhinandrus LeConte	Coelometopini
Tenebrio Linnaeus	Tenebrionini
Zophobas Blanchard	Tenebrionini
Centronopini	
Centronopus Solier	Coelometopini, Tenebrionini
Scotabaenus LeConte	Coelometopini
Tauroceras Hope	Tenebrionini
Acropteronini	
Acropteron Perty	Cnodalonini
Coelometopini	
Alobates Motschulsky	Coelometopini
Apsida Lacordaire	Diaperini
Blapida Perty	Cnodalonini
Bothynocephalus Doyen	Coelometopini
Camaria Serville	Cnodalonini
Choastes Champion	Tenebrionini
Cibdelis Mannerheim	Coelometopini
Cnephalura Doyen	Coelometopini
Cnodalon Latreille	Cnodalonini
Coelocnemis Mannerheim	Coelometopini
Cyrtosoma Perty	Cnodalonini
Dinomus Breme[1]	Misolampini
Elomosda Bates	Cnodalonini
Epicalla Champion	Cnodalonini
Glyptotus LeConte	Tenebrionini
Gonospa Champion	Diaperini
Haplandrus LeConte	Tenebrionini
Hegemona Laporte	Misolampini, Helopini
Hesiodus Champion	Tenebrionini
Hicetaon Champion	Tenebrionini
Ilus Champion	Tenebrionini
Iphthiminus Spilman[2]	Tenebrionini
Isaminas Champion	Misolampini
Isicerdes Champion	Tenebrionini
Merinus LeConte	Tenebrionini
Mitys Champion	Misolampini
Moeon Champion	Cnodalonini
Mophon Champion	Cnodalonini
Mylaris Motschulsky[3]	Tenebrionini
Nesocyrtosoma Marcuzzi[4]	Cnodalonini
Nuptis Motschulsky	Tenebrionini
Oeatus Champion	Tenebrionini
Oenopion Champion	Coelometopini
Othryoneus Champion	Cnodalonini

Table 1. Continued.

Oxidates Champion	Misolampini
Paroeatus Gebien	Tenebrionini
Polopinus Casey	Coelometopini
Polypleurus Eschscholtz	Coelometopini
Saziches Champion	Misolampini
Spinepicalla Pic[1]	Cnodalonini
Stenoboea Champion	Tenebrionini
Sycophantomorphus Pic[1]	Cnodalonini
Upis Fabriceus	Tenebrionini
Xenius Champion	Cnodalonini
Xylopinus LeConte	Tenebrionini
Strongyliini	
Cuphotes Champion	Strongyliini
Mentes Champion	Helopini
Otocerus Mäklin	Strongyliini
Poecilesthus Blanchard	Strongyliini
Pseudotocerus Champion	Strongyliini
Strongylium Kirby	Strongyliini
Talanini	
Talanus Mäklin	Talanini

[1] Not examined or included in key.

[2] *Iphthiminus* Spilman is replacement name for *Iphthinus* (=Iphthimus) of authors. See Spilman (1973).

[3] *Mylaris* Pallas = *Nyctobates* Guerin. See Spilman (1973).

[4] *Nesocyrtosoma* Marcuzzi 1976 (NEW STATUS), originally proposed as a subgenus of *Cyrtosoma,* differs from *Cyrtosoma* s.s. in having the labroclypeal membrane concealed and in having a fossa in each elytron base in which the pronotal base rests. These characters are shared with *Cnodalon* which, like *Nesocyrtosoma,* is endemic to the Greater Antilles.

oninae) are at least superficially similar to those of Phaleriini (subfamily Diaperinae). All of these beetles oviposit in loose, often sandy soil.

Larvae of the tenebrionine tribes are as variable as adults. Body forms similar to that of *Tenebrio,* with a relatively strongly sclerotized body, slightly enlarged prothoracic legs with distinct combs of setae, much enlarged ninth abdominal tergite and annular spiracles are almost ubiquitous in soil-dwelling larvae. However all of these features vary greatly in Tenebrioninae which occupy other situations. For example in Boletophagini the body is grub-like; in Toxicini and Heleini the spiracles are surrounded by peripheral air tubes; in Ulomini and *Lepispilus* (Heleini) the ninth tergite is paraboloid, entirely covering the abdominal apex, with the anus concealed inside it (a similar shape occurs in Alleculinae); and in many Triboliini the setation of the legs is irregular and the forelegs are not enlarged. It has been no more obvious how to subdivide Tenebrioninae on the basis of larval than of adult features. In addition, larvae of many tribes are inadequately described or unknown.

Splitting of Tenebrioninae into several subfamilies may eventually prove desirable (Watt [1974] recognized Toxicinae as a subfamily, for example), but is neither feasible nor practical in a work dealing with only the North and Central American fauna. Therefore, a generally conservative approach is taken here in accepting all the currently recognized tribes without combining them into larger infrasubfamilial units.

Only Tenebrionini, Centronopini, Alphitobiini and Acropteronini, all of which have been confounded with Coelometopini, are formally defined below.

Tribe Tenebrionini, **New Sense**

Tenebronides vrais Lacordaire, 1859 (in part)
Tenebrionini, Reitter, 1920
Tenebrionini, various authors (in part)

Description. Adult.—Small to large (about 6 mm to 30 mm). Eyes moderate in size, weakly emarginated to entirely divided by epistomal canthus; antennae serrate-filiform, weakly incrassate, bearing only simple, setiform sensilla; labrum about twice as broad as long, with basal membrane concealed or exposed; epipharynx asymmetrical (as in Fig. 11; Doyen and Tschinkel, 1982); mandibles with incisors bifid, molas striate or nonstriate; lacinia with or without (*Rhinandrus*) uncus, palp subcylindrical to broadly triangular; tentorium with bridge posterior, slender, not arched. Procoxal cavities closed externally, open or closed internally; mesocoxal cavities closed laterally by mesepimeron; mesosternal apophysis developed as slender dorsal arm with or without anteroventral muscle attachment flange; elytra 9-striate with scutellary striole or estriate. Apical membrane comprising about one-fifth of wing length; recurrent cell large; subcubital fleck present (*Bius*) or absent. Metendosternite with stalk long to short (*Rhinandrus*), tendons inserted near midpoint of arms or close to apex; arms with subterminal muscle attachment flange (much enlarged in *Rhinandrus*). Tarsi clothed ventrally with spinose or pilose (*Zophobas, Rhinandrus*) setae. Ovipositor flexible with coxites and paraprocts subequal in length; coxites divided into four subequal lobes; fourth lobe not digitate; internal female repoductive tract with bursa reduced or absent, spermatheca tubular, coiled, long and slender to short, T-shaped and thick. Aedeagus with mediam lobe freely extrusible or adnate to tegumen (*Zophobas, Rhinandrus*), without accessory lobes. Defensive reservoir short, conical, eversible and with or without (*Bius*) common volume; reservoir walls without annulation, sometimes rigidified by cuticular strip from sternite 7 (see Acropteronini, discussion); secretory ducts distributed over dorsal surface of reservoir, as basal line at neck of reservoir, or as few duct emptying at neck (*Bius*).

Larva.—Cylindrical, moderately sclerotized and pigmented; ocelli present as weak pigment spots without lenses. Antenna with three segments; second segment subequal to basal, about 6–8 times as long as digitate third segment; sensorium single, arcuate around base of third segment, or multiple ellipses (*Zophobas*). Labrum two to two and one-half times as broad as long with anterior margin straight or weakly concave; epipharynx with pair of masticatory processes (right process usually larger), two central blunt spines and 6 annular sensilla (3 sensilla in *Bius*). Mandibles asymmetrical, left with more promient retinaculum and mola; molas variably sculptured with coarse blunt teeth or ridges. Maxilla with mala entire, without uncus; spinose on mediodorsal surface. Hypopharyngeal sclerome with anterior corners prominent, middle straight or weakly bidentate. Prothorax with presternum usually well defined; terga with anterior transverse carina well defined, especially on meso- and metathorax. Legs similar in size and configuration or anterior pair slightly larger, more coarsely spinose (*Zophobas*); at least anterior pair bearing regular combs of spines on inner surface of femur and tibia. Ninth abdominal tergite expanded posteriorly, about two

to three times as long as sternite, sometimes bearing short urogomphi; anus subterminal, below tergite; pygopods moderately large, setose, with posterior surface weakly sclerotized. Spiracles simple ellipses.

Discussion. Tenebrionini as conceived here is greatly reduced from present catalogue listings, with most of the genera transferred to Coelometopini (Table 1). Major differences in ovipositor, internal female reproductive tract, and defensive gland and reservoir structure, as well as a number of other characters (type of antennal sensoria, structure of ninth segment of larvae) separate these groups. These characters are discussed in more detail below under Coelometopini, and most have been previously analyzed several times (Tschinkel and Doyen, 1980; Doyen and Tschinkel, 1982; Doyen et al., in press).

The closest relatives of Tenebrionini are Triboliini and Alphitobiini, whose salient characters have been outlined previously (Doyen, 1985; Doyen et al., in press). As suggested in those publications, it may eventually prove desirable to recognize all three at the subtribal level. Alphitobiini is formally defined below.

Tribe Alphitobiini

Alphitobiini Reitter, 1917

Description. Adult.—Small (about 4 mm to 7 mm). Eyes emarginate but never divided by epistomal canthus; antennae incrassate, bearing stellate, compound sensoria on apical six segments; labrum about two and one-half to three times broader than long, with basal membrane concealed; epipharynx asymmetrical; mandibles with incisors bifid, molas striate or nonstriate; lacinia with uncus; palp narrowly triangular; tentorium with bridge posterior, slender, not arched. Procoxal cavities closed externally and internally; mesocoxal cavities closed by epimeron or sterna; mesosternal apophyses with long, slender dorsal arm without anteroventral muscle flange; elytra 9-striate with scutellary striole. Apical membrane about one-fifth to one-third wing length; recurrent cell large; subcubital fleck present (*Metaclisa*) or absent. Metendosternite with long stalk, tendons inserted near apex of arms; arms with subterminal muscle attachment flange. Tarsi clothed ventrally with spinose setae. Ovipositor as in Tenebrionini; internal female reproductive tract with spermatheca long, slender and coiled (*Metaclisa*) or capsular, reniform. Aedeagus with median lobe adnate to tegmen, without accessory lobes. Defensive reservoirs short, conical, and with common volume or long, saccate, without common volume (*Metaclisa*); secretory ducts distributed over apical half of reservoir (*Metaclisa*) or as basal line on neck.

Larva (based on *Alphitobius*).—Similar in nearly all features to larvae of Tenebrionini, differing as follows: sensorium on second antennal segment arcuate around base of third segment; mandibles with molas of subequal prominence; hypopharyngeal sclerome with anterior margin straight; prothorax without distinct presternum; abdominal tergite nine terminating in single, short urogomphus.

Discussion. Alphitobius adults and Old World *Diaclina* are similar in all diagnostic features. *Metaclisa marginalis* Horn is similar in most features except the defensive reservoirs, which are greatly enlarged and saccate. The secretory tissue drains through many ductules distributed over the dorsal surface of the reservoirs, as in most Tenebrionini. *Metaclisa* is placed in Alphitobiini rather than Tenebrionini because the

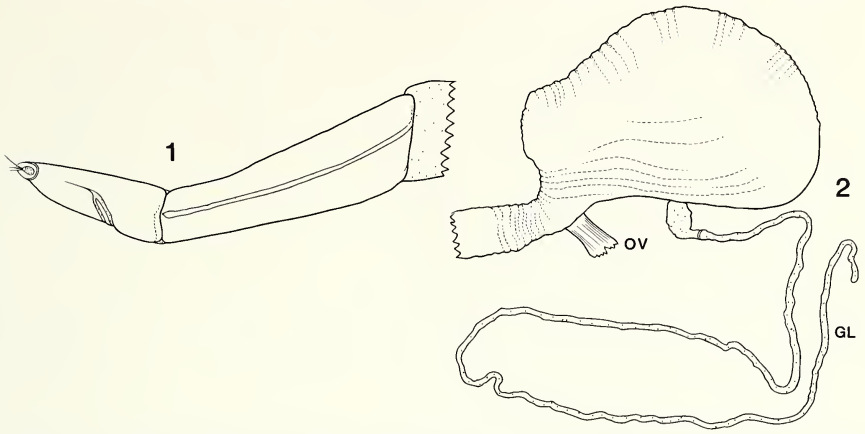
antennae bear compound sensoria and because the median lobe of the aedeagus is adnate to the tegmen. I have not dissected other species of *Metaclisa* (all Old World), which may prove very different from *marginalis,* necessitating a new generic name for the latter.

KEY TO GENERA OF TENEBRIONINI AND ALPHITOBIINI

1. Antenna with compound, stellate sensoria on apical five segments; pronotal margin evenly curved from apex to base (Alphitobiini) 2
— Antenna with simple, setiform sensilla; pronotal margin recurved near base (Tenebrionini) 3
2(1). Epipleuron gradually narrowing to elytral apex; prosternal process prominent, subhorizontal behind coxae; mesosternum acutely concave ..... *Alphitobius*
— Epipleuron abruptly narrowing at anterior margin of visible sternite five, not reaching elytral apex; prosternal process declivous, flattened behind coxae; mesosternum obtusely concave ..... *Metaclisa*
3(1). Tarsi with ventral pads of dense, pilose, yellowish setae; labroclypeal membrane usually exposed, at least medially 4
– Tarsi with stiff, sparse, usually dark colored setae ventrally; labroclypeal membrane concealed 5
4(3). Metasternum about twice length of mesocoxa ..... *Zophobas*
– Metasternum about as long as mesocoxa ..... *Rhinandrus*
5(3). Eye not divided by epistomal canthus 6
– Eye divided by epistomal canthus into dorsal and ventral lobes ..... *Idiobates*
6(5). Elytra with distinct striae 7
– Elytra with confused punctation, without striae ..... *Bius*
7(6). Abdominal sternite five with very fine marginal groove ..... *Neatus*
– Abdominal sternite five without marginal groove ..... *Tenebrio*

Centronopini, new tribe

Description. Adults.—Moderate to large (about 10 mm to 20 mm), elongate, flattened beetles. Eyes moderate in size, strongly emarginated by epistomal canthus; antennae incrassate; apical five or six segments bearing large, stellate sensoria, especially on inner apical margins; labrum about twice as broad as long, with basal membrane concealed; epipharynx symmetrical or nearly so; mandibles with incisors bifid, molas nonstriate; lacinia with uncus, palp weakly triangular; tentorium with bridge posterior, slender, not arched. Procoxal cavities closed externally and internally; elytra 9-striate with short, sometimes poorly defined scutellary striole; mesocoxal cavities closed laterally by mesepimeron; mesosternal apophysis developed as large, anteriorly oriented muscle disk, without dorsal arm. Apical membrane comprising about one-fifth of wing length; recurrent cell large; subcubital fleck absent. Metendosternite with long stalk, tendons inserted slightly beyond midpoint of arms; arms with subterminal muscle attachment flange. Tarsi clothed ventrally with pads of dense, fine, yellowish pubescence. Ovipositor (Fig. 1) strongly sclerotized, slightly compressed in lateral plane with lobing of coxites sometimes obscured and gonostyli papilliform; paraprocts about twice as long as coxites; internal female reproductive tract (Figs. 2, 3) with large bursa copulatrix, long slender accessory gland; spermatheca present or absent. Aedeagus rotated about 45°–60°; median lobe adnate to tegmen or nearly so. Defensive reservoirs (Fig. 4) elongate, without common



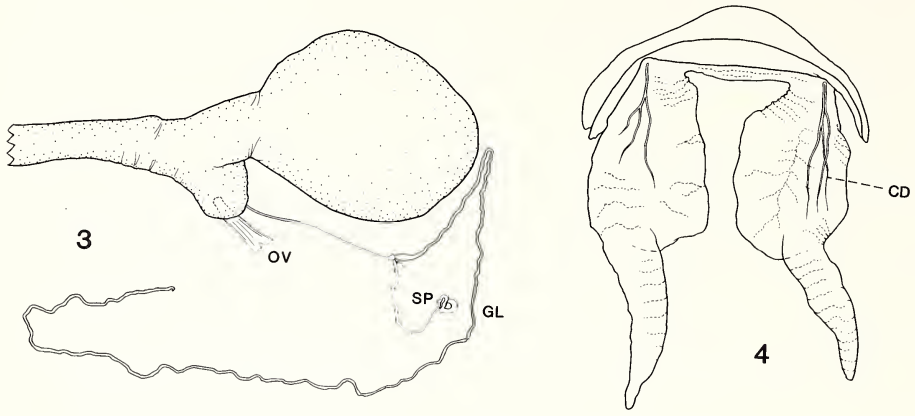
Figs. 1, 2. Female genitalic characters of Centronopini. *Scotobaenus parallelus* LeConte. 1. Ovipositor, lateral. 2. Internal female reproductive tract.

volume; mesal margins slightly expanded at about middle, reservoir walls without annulation; secretions drained by single large collecting duct opening at base of each reservoir.

Larva.—Cylindrical, moderately sclerotized and pigmented; ocelli present as weakly developed pigment spots without lenses. Antenna with three segments; second segment about twice length of basal, bearing sinuate sensorium around base of digitate third segment. Labrum about twice as broad as long with evenly arcuate anterior margin; epipharynx with pair of large masticatory processes (right process larger), two central blunt spines and six annular sensilla. Mandibles asymmetrical, left with more prominent retinaculum and mola; incisors bilobed; molas with several coarse, transverse ridges. Maxilla with mala weakly indented at apex, without uncus; spinose on mediodorsal surface. Hypophryngeal sclerome with middle portion greatly elongate and usually apically bilobed, projecting far anterad of short ligula. Prothorax with distinct presternum; thoracic terga lacking anterior transverse carina. Legs similar in size; bearing combs of spines on inner surfaces of femora and tibiae. Ninth abdominal tergite very large, produced as pair of stout, tapering, sharply pointed urogomphi; ninth sternite small, transverse, bearing short pygopods without spines; anus ventral, usually concealed with pygopods beneath ninth tergite. Spiracles simple annuli or ellipses.

Discussion. Centronopini as defined here comprises *Centronopus* Solier (including *Pyres* Champion), *Scotobaenus* LeConte and *Tauroceras* Hope. Lacordaire (1859) included the first two genera in his Coelometopides, whereas LeConte 1862 and LeConte and Horn (1883), not recognizing Coelometopini, placed them in Tenebrionini. Recent catalogs (Gebien, 1942–1944; Backwelder, 1945; Papp, 1961) place *Centronopus* and *Scotobaenus* in Coelometopini and *Pyres* in Tenebrionini. Spilman (1962a, b) clarified the generic nomenclature, and placed *Pyres* as a synonym of *Centronopus.* Immatures of *Centronopus* have been treated by St. George (1924) and Spilman (1979).

Spilman (1963) described larvae which very likely represent *Tauroceras.* In their



Figs. 3, 4. Internal characters of Centronopini. 3. Internal female reproductive tract of *Centronopus suppressus* (Say). 4. Defensive reservoirs (dorsal) of *Scotobaenus parallelus.*

morphological features these larvae were strikingly similar to those of *Scotobaenus* and *Centronopus.* The most important points of similarity include (1) the strongly sclerotized trunk; (2) the greatly developed middle lobe of the hypopharyngeal sclerome; (3) the distinct combs of setae on the legs; (4) the configuration of the ninth abdominal tergite, with a pair of large urogomphi and several smaller, thorn-like processes. The second and fourth may be considered as synapomorphies of Centronopini, although in *Centronopus* there is a single pair of thorn-like processes on the ninth abdominal tergite and in *Scotobaenus* they are absent.

Tschinkel and Doyen (1980; Appendix IV) noted that the internal female reproductive tract arrangement of *Tauroceras* is of the Tenebrionine type, with separate spermatheca and spermathecal accessory gland. This arrangement also occurs in *Centronopus* (see below). The ovipositor of *Tauroceras* is strongly sclerotized and very similar to that of *Scotobaenus* in the proportions of the coxite lobes. The defensive reservoirs of *Tauroceras* bear annular folds, and cuticular thickenings, whereas those of *Centronopus* and *Scotobaenus* are only irregularly annulate and lack the thickened rings. However, annulate defensive reservoirs have developed independently in several lineages of Tenebrionidae (Tschinkel and Doyen, 1980:332). Although the male secondary sexual characters produce a superficial dissimilarity, the balance of adult and larval features strongly supports the inclusion of *Tauroceras* in Centronopini.

Past disagreements over taxonomic position will perhaps not be laid to rest here because Centronopini have features of both Tenebrioninae and Coelometopinae. Like Coelometopinae the adults have compound sensoria on the apical antennal segments and tarsal pads of fine, dense setae. However, neither of these features is diagnostic of Coelometopinae. Compound antennal sensoria occur also in Diaperinae (Doyen, 1984) and some Tenebrioninae (Amarygmini: Medvedev, 1977; Triboliini: Doyen, 1985; alphitobiini: Doyen et al., in press; also, see above discussion). Tarsal pads of fine, dense setae occur in many Tenebrionidae living on surfaces of logs or trees, including Heleini, Toxicinae, Nyctoporini and Tenebrionini (*Rhinandrus*).

Moreover, features of the defensive glands, internal female reproductive tract and ovipositor preclude membership in Coelometopinae. Though enlarged, as in Coelometopini, and with glands drained by a single collecting duct, the reservoirs of Centronopini (Fig. 4) lack common volume and most lack annulation. The ovipositors of Centronopini (Fig. 1) are slightly compressed in the lateral plane, and quite strongly sclerotized, with reduced gonostyli. The basal coxite lobe is not elongate, as in Coelometopini, nor is the paraproct rotated. The primitive 4-lobed division of the coxite is clearly visible. In *Hegemona* and *Saziches* (placed here in Coelometopini), which have more highly modified, blade-like ovipositors, coxite lobation has been essentially eliminated (Doyen, 1987, fig. 3). The internal female reproductive tract is variable within Centronopini. In *Centronopus* (Fig. 2) and *Tauroceras* the large bursa copulatrix bears a long, slender accessory gland as well as a spermatheca, both attached to a slender, non-glandular duct leading to the vagina near the entrance of the common oviduct. Although differing in detail, this configuration is similar to that of various Tenebrioninae. In *Scotobaenus* (Fig. 3) the bursa copulatrix bears only an accessory gland, somewhat shorter and thicker than in *Centronopus*. This arrangement is like that of *Hegemona* and *Saziches*. The coelometopine tract is similar, except that the apex of the accessory gland forms an enlarged, nonglandular spermatheca. It seems clear that the configuration in *Centropus* and *Tauroceras* is plesiomorphic, that in *Scotobaenus* derived by loss of the spermatheca. In other adult and larval features Centronopini are so similar that it seems almost certain that they represent a monophyletic clade.

Larval characteristics of Centronopini mostly suggest affinities with Tenebrioninae, rather than Coelometopinae. A general tenebrionine feature is the leathery, pigmented cuticle. Most Coelometopinae have more delicate, transparent cuticle. The epipharynx is very similar to that of *Tenebrio,* with a single pair of large, subquadrate masticatory processes. In Coelometopinae, etc., the masticatory processes are usually elongate or dentate, but there is much variation. Centronopini and Tenebrionini also share the presence of a transverse presternum (cervicosternum of Watt, 1970), which is lacking in Coelometopinae I have examined. The legs of larval Centronopini bear regular, longitudinal combs of spines on the femur and tibia, as in most Tenebrionini. In Coelometopinae the leg spines do not form regular combs. Finally, the ninth tergite of Centronopini is much more expanded ventrally than in Coelometopini. The ninth sternite is reduced to a narrow, transverse sclerite, and the ventral anus and pygopods may be concealed within the enlarged tergite. This configuration is very similar to that of *Bassianus* and most Heleini (Matthews and Doyen, in press). In Tenebrionini the ninth sternite is slightly larger, and in Coelometopinae the expansion of the ninth tergite is primarily dorsad and posteriad, so that the anus opens posteriorly and is never concealed within the tergite. The shape of the hypopharyngeal sclerome, with its very long anterior process, is similar to that of Ulomini and Alleculini, but both of these differ in numerous other features from Centronopini.

The character state distributions discussed above show that *Centronopus, Scotobaenus* and *Tauroceras* cannot be retained in Coelometopinae. While not entirely diagnostic, the female reproductive tract and especially the larval characters indicate placement in Tenebrioninae, close to Tenebrionini and Heleini. Apomorphic features distinguishing Centronopini include the sclerotized ovipositor and the anterior process of the hypopharyngeal sclerome.

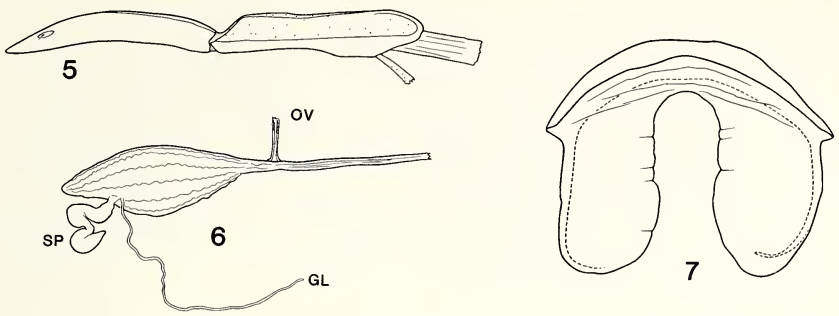
In external characters Centronopini are very similar to typical Coelometopini (compound antennal sensoria; tarsal pads of fine, yellowish setae). For this reason they are included in the keys to that group (see below).

Acropteronini, new tribe

Description. Adult.—Moderate in size (about 6 mm to 20 mm), slender, elongate, subcylindrical beetles. Head deflexed, porrect; eyes large, bulging, anterior border weakly emarginate; antennae slender, basally filiform, becoming weakly serrate apically, bearing simple, hair-like sensilla; labrum about 4 times as broad as long with basal membrane exposed; epipharynx symmetrical or nearly so; mandible with incisor bluntly spatulate, undivided; mola finely, transversely striate; lacinia finely setose, without uncus; palp with apical segment triangular; tentorium with bridge posterior, stout, weakly arched above posterior arms. Procoxal cavities broadly closed externally, open internally. Mesocoxal cavities closed laterally by mesepimeron; elytra with long scutellary striole and 10 complete striae; epipleuron gradually narrowing to apex. Metendosternite with long stalk, stout arms, with tendons located half distance to apex. Apical membrane comprising about one-sixth of wing length; recurrent cell large, subcubital fleck present. Ovipositor with coxites strongly sclerotized, compressed into vertical blade with papillate gonostyli (Fig. 5); paraprocts strongly sclerotized with base transversely expanded; not rotated at rest. Internal female reproductive tract with large bursa copulatrix, long, slender accessory gland and much shorter, thicker spermatheca (Fig. 6). Aedeagus rotated about 90° at rest; median lobe freely extrusible with apex slightly enlarged. Defensive reservoirs small, saccate, with little common volume and without annulation; lateral reservoir walls rigidified by cuticular strip from sternite 7 (Fig. 7); glandular tissue distributed over most of dorsal surface of reservoirs, emptying through diffuse tubules.

Larva and biology.—Unknown.

Discussion. Acropteronini includes only *Acropteron* Perty, which has been included in the tribe Cnodalonini by all authors subsequent to Lacordaire (1859). *Ischyomius* Champion, originally placed in Cnodalonini near *Acropteron* is now included in Pythidae (Lawrence, 1982) or Trictenotomidae (Watt, 1987). As discussed below, Lacordaire's Cnodalonini is based almost entirely on primitive or highly variable characters and cannot be differentiated from Coelometopini. More pertinent here are the important features by which *Acropteron* differs from all members of the Coelometopinae. 1) Only simple, setiform sensilla are present on the antennae of *Acropteron.* Compound sensilla are present in all Coelometopinae, at least on the apical segments. 2) The defensive reservoirs (Fig. 7) are short, saccate structures with the secretory tissue emptying through many tubules distributed diffusely over the dorsal reservoir wall. In most Coelometopinae the reservoirs are elongate, usually with annular foldings in the walls which allow for volumetric expansion. In all Coelometopinae the secretions are delivered through one or a few enlarged collecting tubules which empty near the neck of the reservoirs. In Strongyliini the reservoirs are short and saccate, but none of the other features are similar to *Acropteron.* 3) The internal female reproductive tract of *Acropteron* is of the type found in Tenebrioninae, with separate spermatheca and accessory gland (Fig. 6). In all Coelometopinae there is a single diverticulum from the bursa copulatrix, which is usually expanded apically as



Figs. 5–7. Internal characters of Acropteronini. *Acropteron* sp. (Ex. Sta. Catarina, Brazil). 5. Ovipositor (lateral). 6. Internal female reproductive tract. 7. Defensive reservoirs (dorsal).

the spermatheca. 4) In Coelometopinae the ovipositor is highly specialized, with the paraprocts rotated 180° at rest (see discussion under Coelometopini). In *Acropteron* the ovipositor (Fig. 5) is highly modified as a strongly sclerotized, blade-like organ. The paraprocts do not show any indication of the type of specialization found in Coelometopinae. As noted by Champion (1887:268) and elaborated by Doyen (1987), the ovipositors of *Hegemona* and related genera are sclerotized in the form of two vertical blades. However, in Hegemona the coxites are curved strongly dorsad, whereas in *Acropteron* they are curved ventrad. In several other features *Hegemona* is similar to Coelometopinae (Doyen, 1987). *Talanus* also has a blade-like, sclerotized ovipositor (Tschinkel and Doyen, 1980, fig. 41), but is clearly coelometopine in all other important characters (see below). Thus, all the distinctive apomorphic features of coelometopinae are lacking in *Acropteron.*

Two other unusual features displayed by Acropteron are clearly plesiomorphic and of no use in indicating cladistic relationship. 1) The internally open procoxal cavities occur also in other Tenebrioninae (Heleini, Toxicini and some Tenebrionini) and in Zolodininae. 2) Elytra with ten striae occur also in Lagriinae, Pimeliinae (=Tentyriinae), Zolodininae, and a partial or complete tenth stria occurs in Toxicini (Doyen and Tschinkel, 1982:137). All of these taxa show other apomorphic features not shared with *Acropteron.*

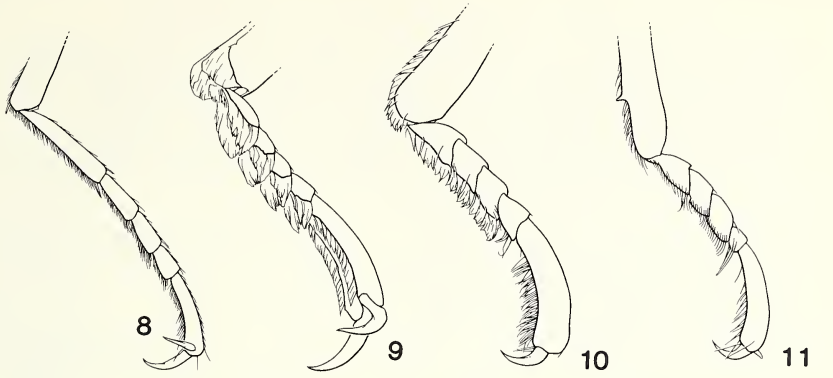
Many of the characteristics discussed above are plesiomorphic and of limited use in determining cladistic position. None, however, disagree with placement in Tenebrioninae. Tenebrioninae are defined to a large extent by lack of derived characters, and division into tribes is problematic. One feature of the defensive reservoirs suggests a possible relationship between various tribes of Tenebrioninae and may be primitive in this subfamily. In *Acropteron* the lateral walls of the defensive reservoirs are stiffened by a strip of cuticle from the seventh abdominal sternite (Fig. 7). A similar strip of cuticle occurs in all genera of Heleini, which have similar short saccate reservoirs. A less well developed strip of cuticle is present in a few Cyphaleini and is also present in *Tenebrio.* Similar strips of cuticle occur in some Opatrini (*Blapstinus, Edylius, Pedinus, Ulus*), and in Alleculinae the neck of the reservoir is sometimes noticeably sclerotized. Both of these latter groups also belong to the tenebrionoid lineage of Doyen and Tschinkel (1982) according to internal characters.

Among primitive Tenebrioninae, *Acropteron* shares a general phenetic similarity with Titaenini (elongate, cylindrical body; deflexed head), but differs in ovipositor, defensive reservoirs and other characters. *Lepispilus* (Heleini) has a rigid, tube-like, sclerotized ovipositor which is somewhat similar to that of *Acropteron,* but shares no obvious synapomorphies. In addition, in *Lepispilus,* the paraproct bases rotate through a partial arc as the ovipositor is exserted or retracted, in a manner analogous to that in Coelometopinae (E. Matthews, pers. comm.). Finally, *Acropteron* differs from all other Tenebrioninae in its extremely broad labrum (about four times broader than long). For the reasons discussed above it is appropriate to recognize Acropteronini as a distinct tribe of Tenebrioninae.

SUBFAMILY COELOMETOPINAE

Description. Adult.—Small to very large (about 5 mm to 45 mm) beetles of diverse shape and color. Antennae filiform, serrate, incrassate or weakly capitate; apical five to eight segments bearing stellate compound sensoria. Labrum transverse with basal membrane exposed or concealed. Mandible with mola finely striate, flat or occasionally coarsely ridged. Maxilla with galea finely setose or with uncus of one or two teeth. Tentorium with bridge posterior, flat or weakly arched. Procoxal cavities broadly closed both externally and internally. Mesocoxal cavities closed laterally by mesepimeron; elytra with scutellary striole and 9 complete striae or estriate. Apical membrane usually comprising about 25% of wing length; recurrent cell moderate to large; subcubital fleck rarely present (e.g., *Upis, Camaria*). Metendosternite with stalk long or short and broad (wingless species), with long arms, usually with tendons inserted near midpoint and subterminal muscle attachment flanges. Tarsi with ventral pads of fine, dense pubescence or with sparser, coarser setae; tibiae frequently with setose inner apical margins. Ovipositor (Tschinkel and Doyen, 1980, figs. 22, 23, 39) with coxites clearly 4-lobed; basal lobe usually elongate (often longer than three apical lobes combined); paraprocts rotated about 145° about articulation with coxite at rest, or, rarely, rotated about 60° to 90° (e.g., *Menephilus,* not North America). Internal female reproductive tract (Tschinkel and Doyen, 1980, figs. 22, 23, 26) consisting of vagina, enlarged bursa copulatrix, and single appendant duct; duct glandular except at apex, which forms spermatheca, which is usually enlarged, subspherical. Aedeagus with tegmen dorsal at rest, rotated about 60° to 90°, or occasionally inverted (rotated 180°); median lobe usually adnate to tegmen, rarely freely extrusible. Defensive reservoirs saccate, with considerable common volume, and often with regular, annular foldings of the walls; defensive tissue draining through one to several enlarged collecting ducts, often with basal ampullae.

Larva.—Elongate, cylindrical, usually with weakly sclerotized trunk segments. Antennae with three segments, second about one to one and one-half times longer than basal, bearing semicircular or occasionally sinuate sensorium around base of digitate third segment. Labrum about as long as wide to twice as long as wide; epipharynx usually with two central spines subtending four to ten annular sensilla and elongate masticatory processes; tormae usually indistinct. Mandibles slightly to moderately asymmetrical, with either left or right mola more prominent; incisor bilobed, usually subtended by retinaculum, giving trilobed appearance. Maxilla with mala entire or weakly (occasionally moderately) indented at apex, sometimes produced medially



Figs. 8–11. Tarsal structure in Coelometopinae. 8. *Coelocnemis* (Coelometopini). 9. *Strongylium* (Strongyliini). 10. *Talanus* (Talanini). 11. *Cyrtosoma* (Coelometopini). Each illustration shows left mesotarsus from anteroventral aspect.

near tip; inner surface spinose. Hypopharyngeal sclerome usually with anterior margin tridentate, occasionally with middle tooth absent or enlarged and produced anterad over ligula. Prothorax without presternum; terga usually lacking anterior transverse carina. Legs similar in size; femoral and tibial setae irregularly distributed, not arranged in regular combs. Ninth abdominal tergite almost always produced as prominent pair of recurved urogomphi, sometimes with additional ridges, spines or calloses. Ninth sternite occupying ventral third of segment with anus subterminal and pygopods small or absent. Spiracles simple annuli or ellipses.

Discussion. By far the most important defining characters of Coelometopinae are those of the ovipositor and internal female reproductive tract, in which intermediacy or exceptions are very uncommon. These features are discussed at greater length under Coelometopini, below. With very few exceptions (see Doyen, 1987, for example), this is one of the most clearly delimited higher taxa of Tenebrionidae, and its definition has been discussed at length in previous publications (Tschinkel and Doyen, 1980; Doyen and Tschinkel, 1982).

Coelometopinae primarily occupy forest and woodland situations in the tropics and subtropics. Larvae inhabit rotten wood, usually when it has reached the punky stage of decay. Less frequently they are found in soil, beneath bark of more recently dead trees or in fruiting bodies of wood-rotting fungi. Adults are frequently found associated with various sorts of dead wood and are usually nocturnal. Loss of wings is common in this group, having led to convergence in body form among distantly related taxa (Doyen et al., in press and following discussion of Coelometopini).

A substantial fauna of Coelometopinae inhabits the hardwood forests of eastern United States. This fauna is largely distinct from the larger Meso-American fauna at the generic level. The western North American fauna is depauperate, with two endemic genera (*Coelocnemis, Cibdelis*) and representatives of a few wide-ranging genera (*Alobates, Iphthiminus, Strongylium*).

The following key includes Centronopini, which is similar to Coelometopini in external features.

KEY TO TRIBES OF COELOMETOPINAE AND CENTRONOPINI

1. Antenna with stellate sensoria (visible at 50× or higher) on apical five or six segments[1]; ventral surface of basal three or four tarsomeres covered by pads of dense, usually yellow pubescence; ventral surface of tarsomeres usually flattened (Fig. 8) 2
– Antenna with stellate sensoria on apical seven or eight segments; ventral surface of tarsomeres covered by stiff, usually dark colored setae; tarsomeres cylindrical, at least on posterior two pairs of legs (Fig. 9) 3
2(1). Tarsomeres three and four subequal, each usually with pad of dense, yellowish pubescence (Fig. 9); body form variable ..... *Coelometopini* and *Centronopini* (part)
– Fourth tarsomere much smaller than third bearing only a few long, ventral setae (Fig. 10); body form elongate, cylindrical ..... *Talanini*
3(2). Prosternal process prominent, horizontal behind coxae; sharply acute and received in deep mesosternal fossa ..... Coelometopini (part)
– Prosternal process declivous, flattened behind coxae; broadly rounded or truncate; mesosternal fossa very broad, shallow .....Strongyliini

Tribe Coelometopini

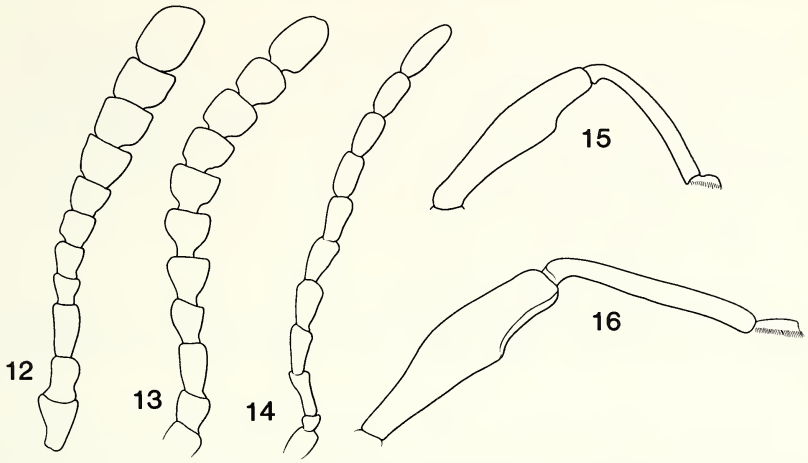
Coelometopini Lacordaire, 1859:358, Doyen et al., in press.
Misolampini Lacordaire, 1859:440.
Nodotelini Koch, 1950:67 (replacement name for Eutelini).
Eutelini Solier, 1844:268 (not Walker, 1834; see Koch, 1950).
Cnodalonini Lacordaire, 1859:414.
Tenebrionini, various authors (in part).
Hegemonini Reitter, 1922:5.

Description. Adult.—Small to very large (about 5 to 45 mm) beetles of diverse body shape and color. Eyes reniform, moderate in size, separated dorsally by much more than width of single eye lobe. Antennae incrassate or weakly capitate, with stellate sensoria on apical five to six (rarely seven or eight) segments. Labral membrane exposed or concealed. Tarsi with ventral surface almost always flattened, bearing pads of yellowish, usually pilose setae; inner margins of tibiae frequently pilose, especially near apices. Ovipositor a flexible tube or rarely (*Hegemona, Saziches*) flattened, blade-like and strongly sclerotized; spermatheca swollen, spherical or rarely (*Mylaris*) isodiametric with accessory gland. Aedeagus with median lobe adnate to tegmen (freely extrusible in *Tauroceras*. Defensive reservoirs elongate, walls usually with annular folds (folds absent or rudimentary in *Apsida, Camaria*).

Larva.—Moderately elongate, cylindrical or subcylindrical; ninth abdominal tergite usually with promient recurved urogomphi, rarely (*Coelocnemis*) with ring of accessory spines.

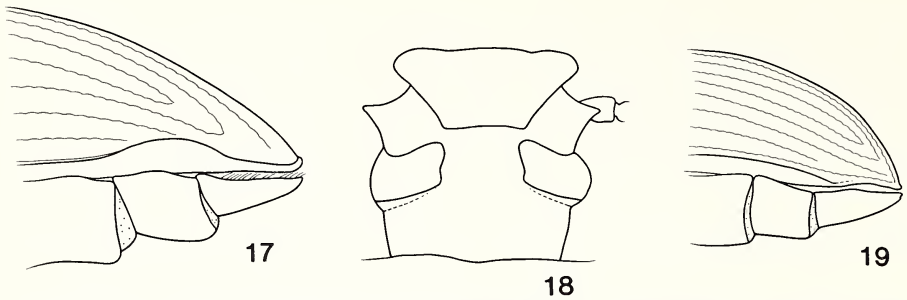
Discussion. In catalogues and checklists most coelometopine genera are listed under tenebrionini, which are extremely different in several important internal features. 1)

[1] Stellate sensoria appear at 25× to 50× as rounded, dome-shaped structures set in shallow pits on apical antennal segments. They are especially prevalent on the inner apical margins of the antennomeres. Above 50× their stellate configuration may be discernible, particularly in larger specimens.



Figs. 12–16. Antennal and leg variation in Coelometopinae. 12. *Apsida.* 13. *Othryoneus.* 14. *Mophon,* all from dorsal aspect. 15. *Isicerdes.* 16. *Choastes,* both from anterior aspect.

In Tenebrionini the defensive reservoirs are short saccate with the secretion collecting ducts emptying diffusely through the dorsal surface (as in Fig. 7). The reservoir walls lack annular folds and are eversible. In Coelometopini the defensive reservoirs are elongate with one or a few collecting ducts emptying at the neck. The reservoirs are never eversible and their walls almost always have annular folds which allow expansion (Tschinkel and Doyen, 1980, fig. 14e). 2) The ovipositor of Tenebrionini consists of a pair of basal paraprocts, subequal in length to the coxites (Doyen, 1966, figs. 71, 72). The coxites are subdivided into four subequal lobes. In Coelometopini the paraprocts are much shorter than the coxites, and at rest are rotated 180° so that the morphologically proximal ends lie distally beside the coxites (Tschinkel and Doyen, fig. 39). The proximal coxite lobe is longer than the distal lobes—often considerably longer than the three distal lobes combined. 3) In Tenebrionini the spermatheca and the spermathecal accessory gland are separate structures, either opening independently into the bursa copulatrix, or with the spermatheca emptying very near the base of the accessory gland (Tschinkel and Doyen, 1980, figs. 33, 34). In Coelometopini the apex of the accessory gland is nonglandular and functions as the spermatheca. In nearly all genera the apex is greatly dilated and spherical (Tschinkel and Doyen, fig. 26). 4) The aedeagus of Tenebrionini has a connecting membrane between the median lobe and tegmen, allowing free extrusion of the median lobe. The median lobe extrudes below the tegmen. In Coelometopini the connecting membrane is almost always very short or absent, so that the position of the median lobe is fixed or nearly so relative to the tegmen. The aedeagus is usually rotated so that the median lobe is lateral or ventrolateral to the tegmen. 5) In Tenebrionini the antennae bear simple, setiform sensilla on all the segments. (Compound sensoria are present in closely related groups such as Alphitobiini and Triboliini, however.) In Coelometopini, in addition to setiform sensilla, there are compound, stellate sensoria on the apical five to eight segments (see Medvedev, 1977, figs. 31–55). These char-



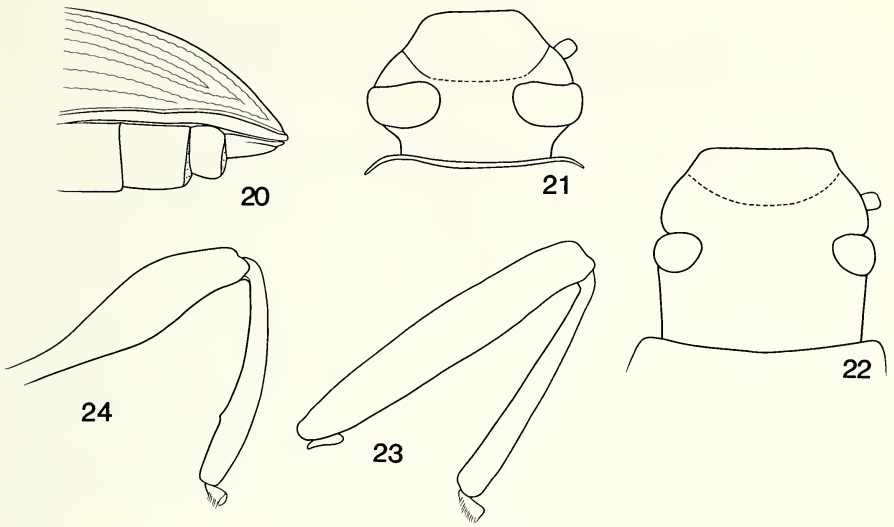
Figs. 17–19. Taxonomic characters of Coelometopini. 17. Elytral apex of *Tauroceras,* left lateral aspect. 18. Head of *Tauroceras* female, dorsal. 19. Elytral apex of *Haplandrus fulvipes* Herbst.

acters are discussed in much greater detail in previous papers (Tschinkel and Doyen, 1980; Doyen and Tschinkel, 1982). Several larval differences between Coelometopini and Tenebrionini are discussed above under Centronopini.

The genera assigned here to Coelometopini are split between Misolampini, Cnodalonini and Coelometopini in catalogues. As pointed out earlier (Doyen et al., in press) Misolampini and Cnodalonini have not been redefined since Lacordaire (1859) originally proposed them on the basis of very superficial characters. Misolampini (and the Old World Nodotelini) simply comprise conglomerations of flightless Coelometopini, and it is now clearly evident that flightlessness has evolved independently dozens or even hundreds of times in Tenebrionidae. Certain of the "misolampine" genera appear to be closely related. Examples include *Isaminas, Sphaerotus* Kirby, *Immedia* Pascoe, *Hemimedia* Gebien and *Parimmedia* Gebien in the neotropics or *Hegemona, Saziches* and *Promorphostenophanes* Kaszab in the neotropics and oriental region respectively (Doyen, 1987). The latter group would correspond to Hegemonini of Reitter (1922). Other groups of genera, however, have certainly been derived from different parts of Coelometopini (e.g., *Heliofugus* Guerin, *Myrmecodema* Germain, *Mitys* Champion). *Misolampus* Latreille, from the Mediterranean region, differs from the most similar New World genera in several salient features, including the complete internalization of the scutellum, in the much shorter legs and partially exposed labral membrane, and in having the epipleural margins subparallel throughout, rather than broadened basally. It seems likely that *Misolampus* is more closely related to *Coelometopus,* which it resembles in general body form, than to any New World genus, but their exact derivation from winged forms is unclear. The genera discussed above all possess the complete inventory of diagnostic Coelometopine traits without significant variation.

Diceroderes Solier, from Mexico, appears in catalogs under Eutelini (=Nodotelini). Properly, that genus, along with *Ozolais* and *Calymmus,* belongs in Toxicini (Doyen, 1988; Doyen et al., in press). In addition to the evidence cited above I have associated toxicine type larvae with *Diceroderes.*

Cnodalonini Lacordaire is based on *Cnodalon* Latreille, which possesses all the important internal and external features of Coelometopini. Tschinkel and Doyen (1980) recognized cnodalonine categories for defensive reservoir configuration (res-



Figs. 20–24. Taxonomic characters of Coelometopini. 20. Elytral apex of *Hicetaon.* 21. Head of *Epicalla,* dorsal. 22. Same, *Merinus.* 23. Mesothoracic leg of *Alobates,* anterior. 24. Same, *Merinus,* male.

ervoir walls lacking annular folds), ovipositor (coxite lobes three and four fused), and internal female reproductive tract (spermatheca isodiametric with accessory gland. These distinctions were based on examination of other genera placed in Cnodalonini in catalogs. For example, defensive reservoirs of *Camaria, Hapsida* and several Old World genera lack annular folds. Likewise, *Hapsida* and several Old World "cnodalonines" have coxite lobes three and four fused, and the latter do not have the spermatheca enlarged. Examination of additional taxa and characters shows that none of these character states is distributed in a recognizably systematic fashion. For example, while the defensive reservoirs completely lack annulation in *Hapsida,* they distinctly show basal annulation in *Camaria* and *Blapida* becoming nonannulate distally, especially in the latter. In *Epicalla,* phenetically similar to *Camaria,* the reservoirs are fully annulate. Again, examining the structure of the internal female reproductive tract, a non-enlarged spermatheca occurs in *Apsida, Taphrosoma, Eucyrtus* and *Hemicera. Taphrosoma* was previously classified in Tenebrionini, and is phenetically very different from the other genera. *Hapsida* contains highly specialized beetles previously classified as Diaperini (e.g., Triplehorn, 1965, 1970), and the other two genera are Old World. Nor are the "cnodalonine" character states highly correlated with one another: only *Hapsida, Eucyrtus* and *Hemicera* share all three "cnodalonine" states. While Hemicera and *Eucyrtus* may be closely related, *Hapsida* is very different. In general it seems likely that all three of the "cnodalonine" characters are subject to convergence or else represent primitive retained characteristics.

Thus, there is no morphological basis for recognizing a tribe Cnodalonini. Even if some of the more distinctive "cnodalonine" genera, such as *Hapsida* or the group related to *Camaria,* are eventually recognized, Cnodalonini could not be used no-

menclaturally since *Cnodalon* clearly belongs to the Coelometopini *sensu stricto* according to all diagnostic characters. *Metaclisa marginalis,* the only North American genus assigned to Cnodalonini, belongs to Tenebrioninae-Alphitobiini, discussed above.

The genera included here in Coelometopini are listed in Table 1, where the former tribal association and pertinent references are also indicated. In this combined sense Coelometopini comprises one of the major groups of Tenebrionidae, and certainly one of the most variable, especially in tropical regions. Understanding its patterns of variation and producing a meaningful generic classification remains a major task.

As in most large groups of organisms, not all genera of Coelometopini are equally easy to identify using keys. The following key is constructed so that several genera with intermediate or equivocal character states may be identified by following either alternative of the pertinent couplet. This is usually the reason that a taxon appears more than once in the key. In a few cases the genera as now conceived are polymorphic for the key characters, accounting for their multiple appearance in the key. This is the situation with *Cibdelis,* for example, where the epistomal border is emarginate in *C. bachei,* often exposing the labro-clypeal membrane. In *C. blaschkei* the epistomum is not emarginate and the membrane is concealed.

KEY TO GENERA OF COELOMETOPINI AND CENTRONOPINI

1.	Labroclypeal membrane concealed beneath epistomum	7
–	Labroclypeal membrane broadly exposed just before epistomal margin	2
2(1).	Tarsus with setal pad on penultimate segment much smaller than on preceding segments (Fig. 11), consisting of a narrow, apical fringe; lateral margins of pronotum dentate	*Cyrtosoma*
–	Tarsus with setal pad on penultimate segment similar to those on preceding segments (as in Fig. 9); lateral margins of pronotum not dentate	3
3(2).	Pronotum with base margined; antennae filiform, moniliform or gradually clavate (Figs. 12–14), with segments eight and nine subquadrate or longer than broad	4
–	Pronotum with base unmargined; antennae clavate (Fig. 12), with segments eight and nine about twice as broad as long	*Apsida*
4(3).	Prosternal process prominent, subhorizontal or horizontal behind coxae; mesosternum deeply excavate	5
–	Prosternal process declivous immediately behind coxae; mesosternum very shallowly excavate, nearly flat	*Cibdelis*
5(4).	Antenna slender, filiform, much longer than head and prothorax combined (Fig. 14)	6
–	Antenna submoniliform (Fig. 13), shorter than head and prothorax combined	*Othryoneus*
6(5).	Eye with deep groove extending around apex of ventral lobe; epipleuron terminating abruptly at about anterior margin of fifth visible abdominal sternite	*Mophon*
–	Eye with groove extending medially behind maxillary articulation from apex of ventral lobe of eye; epipleuron extending to elytral apex	*Elomosda*
7(1).	Elytra with apices conforming to shape of last abdominal sternite	9
–	Elytra with apices produced beyond last abdominal sternite as spine-like processes	8

8(7). Foretibia strongly curved ventrad in apical third; metasternal length about equal to coxal diameter 41
– Foretibia nearly straight; metasternal length at least twice mesocoxal diameter ..... *Blapida*
9(7). Metafemur abruptly emarginate on apical ¼ to ⅛ of inner surface (Figs. 15, 16); often with small spur or prominence just basad of emargination 10
– Metafemur with margins subparallel or gradually convergent toward apex, never abruptly emarginate 14
10(9). Body length greater than 3 cm; fifth visible abdominal sternite with marginal groove ..... (some males of) *Mylaris*
– Body length less than 2 cm; fifth visible sternite without marginal groove ... 11
11(10). Metasternal length about ⅓ to ½ diameter of mesocoxa; all femora with spur on inner surface ⅔ distance to apex ..... *Cnephalura*
– Metasternal length about 1.5 times diameter of mesocoxa; spurs present or absent from inner femoral surface 12
12(11). Metatibia arcuately curved (Fig. 15); prosternal process horizontal or subhorizontal behind coxae ..... *Isicerdes, Ilus*
– Metatibia straight except just before articulation with femur; (Fig. 16) prosternal process declivous behind coxae 13
13(12). Metafemora reaching anterior margin of fifth abdominal sternite; mesosternal fossa with margins strongly elevated, dentiform ..... *Choastes*
– Metafemora reaching at most to anterior margin of fifth abdominal sternite; mesosternal fossa with margins slightly raised ..... *Hesiodus*
14(9). Head with abrupt, arcuate escarpment across frons between eyes; eye with supertending groove, expanding into a large deep excavation behind eye ... . *Bothynocephalus*
– Head with frons uniformly curved or with epistomal region slightly depressed below level of frons; head sometimes with grooves along dorsal margin of eye, but never with large pits 15
15(14). Epipleuron abruptly broadened at fourth visible abdominal sternite then narrowed to elytral apex (Fig. 17); epistoma produced as sharp projection between eye and lateral epistomal suture; clypeus produced laterally much beyond epistomal suture (Fig. 18) (Centronopini) ..... *Tauroceras*
– Epipleuron with margins subparallel or gradually converging posteriorly (sometimes abruptly narrowing at about anterior margin of fifth abdominal sternite) (Figs. 19, 20); epistoma evenly arcuate between eye and lateral epistomal suture; clypeus not produced laterally beyond epistomal suture 16
16(15). Dorsal lobe of eye with marginal groove around apex 17
– Dorsal lobe of eye without groove around apex 29
17(16). Metasternal length between coxae 1.5 to 2 times mesocoxal diameter 20
– Metasternal length between coxae equal to or less than mesocoxal diameter 18
18(17). Tibiae with paired, narrow longitudinal lines of yellowish pubescence on apical ½ to ⅔ of inner surfaces 30
– Tibiae without lines of pubescence, or with apical ⅛ to ¼ with faint setal lines or patch 19
19(18). Legs long, metafemur reaching at least to base of fifth abdominal sternite, frequently extending beyond apex of abdomen 42
– Legs shorter, metafemur reaching no farther than third abdominal sternite ..... *Polypleurus*
20(17). Epipleuron complete to apex of elytra, gradually narrowed posteriorly from fifth abdominal sternite (Fig. 20) 22

– Epipleuron abruptly narrowing at about anterior margin of fifth abdominal sternite, disappearing before elytral apex (Fig. 19) 21

21(20). Mesosternal fossa deep, with lateral margins strongly raised; pronotal base with complete, raised margin ..... *Sthenoboea*

– Mesosternal fossa broad, shallow, with lateral margins scarcely raised; pronotal base unmargined, at least medially ..... *Haplandrus*

22(20). Fifth abdominal sternite without marginal groove or line 25

– Fifth abdominal sternite with marginal groove or impressed line 23

23(22). Frons behind epistomal suture much more coarsely punctate than posteriorly and around eyes ..... *Hicetaon*

– Frons finely, evenly punctate 24

24(23). Fifth abdominal sternite with groove deeply excavate; mentum flat ..... *Oeatus*

– Fifth sternite with fine, slightly impressed marginal line; mentum elevated as a prominent tubercle anteriorly ..... *Glyptotus*

25(22). Femora strongly clavate; profemur 2.5 to 4 times thicker in middle than at base 27

– Femora subcylindrical; profemur no more than 2 times thicker in middle than at base 26

26(25). Epistomal suture faint in medial portion, shallowly impressed or obsolete ... 34

– Epistomal suture very deeply incised in medial portion ..... *Paroeatus*

27(25). Pronotum finely and shallowly punctate (punctures much smaller than single eye facet); elytra punctate-striate 28

– Pronotum coarsely and deeply punctate (punctures as large as several eye facets combined); elytra reticulately rugose ..... *Upis*

28(27). Epistomal suture strongly incised ..... *Nuptis*

– Epistomal suture very fine, shallow, sometimes partially obsolete, never incised ..... *Merinus*

29(16). All tibiae with paired, narrow longitudinal lines of yellowish pubescence on apical ½ to ⅔ of inner surface 30

– Tibiae without lines of pubescence or with apical ⅛ to ¼ sometimes with single faint setal lines or with setal patch 31

30(18, 29). Gena with deep, abrupt excavation at apex of ventral lobe of eye .... *Oenopion*

– Gena often coarsely rugose but never with distinct excavation at apex of ventral lobe of eye ..... *Coelocnemis*

31(29). Antenna gradually enlarged or serate-filliform (as in Figs. 13, 14); segments nine and ten no more than 1.5 times as broad as long 33

– Antenna with apical five or six segments enlarged as more-or-less distinct club (Fig. 12); segments nine and ten about twice as broad as long 32

32(31). Elytral base broader than base of thorax; epipleuron expanded as prominent umbo at elytral base; elytra coarsely punctate-striate ..... *Cnodalon*

– Elytral and thoracic bases equally broad; epipleuron not forming umbo; strial punctures of elytra extremely fine ..... *Gonospa*

33(31). Epipleuron gradually narrowing posteriorly, with subparallel margins throughout except near humerus and apex (Fig. 20); extending to elytral apex or nearly so 40

– Epipleuron abruptly narrowed at about anterior margin of fifth abdominal sternite; not reaching elytral apex (Fig. 19) 34

34(26, 33). Prosternal process horizontal, prominent behind coxae; mesosternum deeply excavate with raised lateral borders 35

– Prosternal process declivous; mesosternum very shallowly excavate, lateral borders not raised 36

35(34). Elytral interstices smooth; antenna extending posteriorly beyond eyltral base 36
– Elytral interstices bearing large, shining tubercles; antenna not reaching base of prothorax ..... *Xenius*
36(35). Elytral length no more than 1.5 times width; pronotum with continuous raised margin around lateral and posterior borders ..... *Nesocyrtosoma*
– Elytral length more than twice width; pronotum with submarginal groove along lateral border, becoming deeper posteriorly and interrupting raised margin at corner ..... *Moen*
37(34). Femora clavate; profemur about twice as thick in middle as at base ..... (Centronopini) 39
– Femora subcylindrical; profemur less than 1.5 times thicker in middle than at base 38
38(37). Metasternum length between coxae 1.5 to 2 times mesocoxal diameter 50
– Metasternum length between coxae less than mesocoxal diameter ..... *Cibdelis*
39(37). Fifth visible abdominal sternite with marginal groove ..... *Scotobaenus*
– Fifth visible abdominal sternite without marginal groove ..... *Centronopus*
40(34). Metasternum length between coxae about 1.5 to 3 times mesocoxal diameter 47
– Metasternum length between coxae equal to or less than coxal diameter 41
41(8, 40). Legs long, metafemur reaching fifth abdominal sternite or beyond 42
– Legs shorter, metafemur reaching third or fourth abdominal sternite *Polopinus*
42(19, 41). Metatarsus excluding claw at least ¾ length of tibia 43
– Metatarsus shorter, almost always about half length of tibia 44
43(42). Antenna with segments three and four subequal in length; segments six to ten about three times as long as wide; body more than 2 cm long ..... *Hegemona*
– Antenna with segment three about 1.5 times longer than segment four; segments six to ten about twice as long as wide; body less than 15 mm long .. .. *Saziches*
44(42). Prosternal process horizontal, prominent behind coxae, fitting into deep mesosternal fossa with strongly raised lateral margins 45
– Prosternal process subhorizontal or declivous; mesosternum very shallowly concave or flat, with lateral margins not raised 46
45(44). Epistomal suture deeply impressed at angles anteromedial to eyes, usually forming distinct foveae ..... *Isaminas*
– Epistomal suture shallow throughout its course, never deeper at angles *Oxidates*
46(44). Mentum with anterior central portion elevated as a forward projecting tubercle ..... *Mitys*
– Mentum almost flat, never with anterior elevation ..... *Cibdelis*
47(40). Head constricted abruptly just behind eyes, much narrower than before eyes (Fig. 21) 48
– Head with lateral margins subparallel or gradually narrowed, not abruptly constricted behind eyes (Fig. 22) 50
48(47). Prosternal process horizontal or subhorizontal, prominent behind coxae; received in deep fossa with raised lateral borders in mesosternum 49
– Prosternal process declivous behind coxae; received in shallow, obtuse fossa without raised lateral margins 53
49(48). Medial epistomal suture in broad, shallow depression with shallow fovea before each eye; head anterad of eyes shorter than width of dorsal eye lobe ..... *Epicalla*

– Medial epistomal suture not depressed; no foveae or depressions before eyes; head anterad of eyes longer than width of dorsal eye lobe ..... *Camaria*

50(38, 47). Pronotal base with complete raised margin 51

– Pronotum with base unmargined, at least medially ..... *Haplandrus*

51(50). Basal four tarsomeres with ventral surface entirely covered by pads of dense pubescence 52

– Tarsomeres with two longitudinal rows of setae, separated by groove with few sparse setae ..... *Iphthiminus*

52(51). Elytra regularly striate (strial punctures sometimes very fine) 53

– Elytra irregularly rugose; striae not discernible ..... *Upis*

53(52). Fifth abdominal sternite without marginal groove 55

– Fifth abdominal sternite with marginal groove 54

54(53). Epistomal margin arcuately concave; head constricted behind eyes; more than 2.5 cm long ..... *Mylaris*

– Epistomal margin nearly straight; head not constricted behind eyes; less than 2 cm long ..... *Xylopinus*

55(54). Meso- and metatibia arcuately curved (Fig. 23); pronotum with hind angles rounded ..... *Merinus*

– Meso- and metatibia straight (Fig. 24); pronotum with hind angles sharp, right angled ..... *Alobates*

Tribe Strongyliini

Strongyliides Lacordaire, 1859 and various authors.
Strongyliini, various authors.

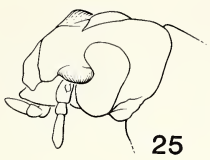
Description. Adult.—Very small to moderate (about 3 mm to 20 mm) beetles, usually with elongate, subcylindrical body; color highly variable. Eyes large, usually separated dorsally by less than width of single eye lobe, frequently contiguous or nearly so, especially in males. Antennae usually serrate, sometimes weakly incrassate, rarely pectinate; apical seven or eight segments bearing stellate, compound sensoria. Labral membrane exposed. Tarsi nearly cylindrical, ventral surfaces usually covered by stiff, often dark colored setae; tibiae seldom bearing strips or patches of pile. Ovipositor a flexible tube; spermatheca swollen, spherical. Aedeagus with median lobe adnate to tegmen or only slightly extrusible. Defensive reservoirs short saccate, without annular folds.

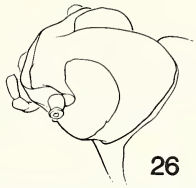
Larva.—Very elongate, cylindrical or nearly so; tergite nine rigidly sclerotized, formed into pair of large, apically bifid, recurved urogomphi, supertended anteriorly by a serrate, transverse ridge; tergite eight rigidly sclerotized, sometimes with transverse ridge or denticles; sternites eight and nine less rigidly sclerotized.

Discussion. Many Strongyliini are brightly metallic or pastel, as in some Coelometopini. In the structure of the defensive glands there is no confusion between the tribes, at least in the New World fauna.

All Strongyliini have stellate sensoria on the terminal seven or eight antennal segments. Among north and central American Coelometopini stellate sensoria occur on the terminal five or six segments, with the exception of *Mophon,* where they are borne on the apical eight segments.

The form of the ninth abdominal segment of larval Strongyliini is superficially similar to that of some Coelometopini such as *Coeloenemis,* where a row of complex spines supertends the urogomphi. In *Coeloenemis,* however, tergite nine becomes weakly sclerotized anteriorly, and segment eight and sternite nine are no more strongly





Figs. 25, 26. Cranial structure in Strongyliini. 25. Oblique aspect of head of *Strongylium*. 26. Same, *Mentes*.

sclerotized than the preceding segments. Triplehorn and Spilman (1973) described larvae of four species and pupae of two species of North American *Strongylium*.

Mentes has been placed in the Helopini on the basis of Champion's (1893) vague statement that it was probably a "degraded" member of that tribe. I have been able to dissect only males, whose antennae have stellate, compound sensoria on segments three to eleven, and whose defensive glands are of the short saccate type of Strongyliini, with much common volume and without annulation. In Helopinae compound sensoria are never present on the antennae, and the defensive reservoirs are elongate, medially expanded and without common volume (Tschinkel and Doyen, 1980). On the basis of these characters I am placing *Mentes* in Strongyliini, and I predict that when observed the ovipositor and internal female reproductive tract will support this transfer.

Without a detailed study it is impossible to judge the cladistic relationship of *Otocerus* or *Pseudotocerus* to Strongylium. They are separated in the following key according to the characters used by Champion (1888). In this regard the other small genera of Strongyliini described by Pic and others must also be suspected as specialized derivatives of *Strongylium,* whose New World species are unrevised since the work of Mäklin (1862). The Chilean genus *Homocyrtus* Reitter, placed in Strongyliini in catalogues, is a member of Chalcodryidae (Watt, pers. comm.; Doyen, unpublished).

KEY TO STRONGYLIINI

1. Antenna with apical 5 or 6 segments much broader than long, forming a more or less distinct club 2
– Antenna with all segments longer than broad, filiform to serrate 3
2(1). Pronotum margined ..... *Poecilesthus*
– Pronotum not margined ..... *Cuphotes*
3(1). Antenna inserted beneath strong epistomal canthus; canthus laterally elevated, emarginating eye posterior to antennal base (Fig. 25); antennae usually filiform 4
– Antenna inserted within emargination in eye; epistomal canthus very weak, narrow (Fig. 26); antenna serrate or pectinate, especially in males ..... *Mentes* Champion
4(3). Antenna with segment three much shorter than segment four; medial apical angles of antennal segments four to ten usually produced, giving a serrate appearance 5
– Antenna with segment three as long or longer than segment four; segments four to ten usually filiform ..... *Strongylium*
5(4). Hind femur reaching apex of elytra; basal segment of hind tarsus 2 to 3 times as long as apical segment ..... *Pseudotocerus*
– Hind femur shorter, not reaching apex of elytra; basal segment of hind tarsus 1 to 2 times as long as apical segment ..... *Otocerus*

Tribe Talanini

Talanites Champion, 1887.
Talanini, various authors.
Dignamtini LeConte and Horn, 1883.

Description. Adult.—Small to moderate (about 3 mm to 10 mm). Eyes moderate to large, bulging, but separated dorsally by much more than width of dorsal eye lobe. Antennae incrassate, bearing stellate, compound sensoria on apical five or six segments. Labral membrane exposed. Tarsi with ventral surface flattened, with pads of yellowish, pilose setae; fourth tarsomere of first two pairs of legs much smaller than preceding tarsomeres and bearing only few long setae. Inner tibial surface setose or pilose. Ovipositor strongly sclerotized, laterally compressed, without apparent gonostyli or lobing of coxite (Tschinkel and Doyen, 1980, fig. 41); spermatheca swollen, spherical. Aedeagus with median lobe slightly extrusible. Defensive reservoirs large, saccate, constricted at neck, without annular folds.

Larva.—Unknown.

Discussion. Talanini contains only the Neotropical genus *Talanus,* which universally possesses a highly modified, blade-like ovipositor, superficially similar to those in *Hegemona, Saziches* and *Acropteron.* In *Talanus,* however, the paraproct has the ability to rotate about its articulation with the coxite, as in nearly all Coelometopinae. In the others the paraproct cannot rotate, and they differ in numerous other important characters, as discussed above. *Talanus* lacks compound sensoria on antennal segments four and five, and has the tarsi ventrally pilose, differentiating it from Strongyliini, near which it is usually placed in catalogues. The lack of annulation on the defensive reservoir walls is shared with *Apsida* and *Camaria* among the New World Coelometopini, and in *Apsida* the penultimate tarsomere is smaller than the antipenultimate and has reduced pilosity, as in *Talanus. Talanus* differs from both of these in numerous other characters, however, and must be accorded an isolated position within Coelometopinae. Talanini has been long recognized, and unless more compelling evidence can be marshalled for derivation from some other tribe, it should be retained for these strongly apomorphic beetles.

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